EFFECT OF TEMPERATURE ON THE RESPIRATION RATE AND THE RESPIRATORY QUOTIENT OF SOME VEGETABLES[1]

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(WITH SEVEN FIGURES)

Introduction

Numerous experiments have been conducted to determine the respiration rates of various vegetables after harvest. Nevertheless, it is well-nigh impossible to gain a clear knowledge of the comparative rates of respiration exhibited by different kinds of vegetables from the scattered data in the literature, because of the wide variations in temperature and other conditions under which such experiments were carried out. Only the studies of BENOY (**4**) and of APPLEMAN and SMITH (**1**) represent consistent efforts to secure comparable data on respiration under uniform conditions.

Aside from transpiration, respiration is undoubtedly the most important factor contributing to the deterioration of vegetables after harvest. Additional information on respiration rates at different temperature levels is needed for the solution of practical problems concerned with storage and transportation of fresh vegetables. The experiments here reported were carried out with this point in view. Carbon dioxide production and oxygen consumption were determined simultaneously in the hope that the calculated respiratory quotients would shed some light on the metabolism involved. In particular, it was expected that an explanation might be found for the phenomenon of low temperature injury which has frequently been observed in certain fruits and vegetables and which has been attributed to abnormalities in the course of respiration.

Methods

The procedure followed was to measure simultaneously the rate of oxygen uptake and carbon dioxide evolution, and was essentially the same as that developed by MAGNESS and DIEHL (**12**). Suggestions for the improvement of this method offered by HALLER and ROSE (**9**) were followed and the writer further changed the apparatus by applying the principle of the Mariotte bottle in order to maintain a uniform atmospheric pressure in the system.

Depending on the temperature of the room and the respiratory activity of the vegetable under examination, a representative sample, varying from 200 to 3000 gm., was placed in the respiration chamber (E) (fig. 1). After

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applying the cover, the air in the chamber was saturated with water vapor by means of a hand atomizer. Through the funnel (D) 50 ml. of 1 N sodium hydroxide were added to the funnel (F). The chamber was then connected to the oxygen cylinder (B) and this in turn was attached to the Mariotte bottle (A).

Carbon dioxide produced in the course of respiration was absorbed by the alkali in the bottom of the chamber. As oxygen was consumed by the vegetables, the gas pressure in the chamber diminished and this caused a flow of oxygen from the cylinder (B) into the chamber. Atmospheric pressure in the entire system was quickly reestablished by the flow of water from the Mariotte bottle into the oxygen cylinder. This arrangement proved to be so sensitive that a pressure deficit of only one or two mm. of water as read on the manometer (H) was sufficient to cause water to enter the cylinder. It should be pointed out that the actual height of the water level in the

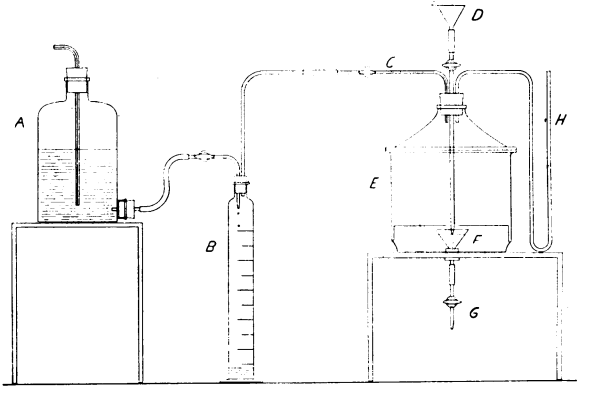

FIG. 1. Apparatus used to measure simultaneously oxygen consumption and carbon dioxide production during respiration.

Mariotte bottle has no effect on the pressure in the system and atmospheric pressure is maintained as long as the lower tip of the capillary tube in A is kept at the same level as the tip of the delivery tube entering the cylinder (B).

At the end of each run the quantity of oxygen displaced by water in the cylinder (B) was measured. At the same time, the alkali in the funnel (F) was drawn off, an excess of barium chloride was added, and the amount of carbonate present determined by double titration against 1 N hydrochloric acid using phenolphthalein and methyl orange as indicators.

A serious error in the oxygen readings arises from the fact that changes in atmospheric pressure and temperature produce volume changes in the system which at low temperatures occasionally exceed those resulting from the consumption of oxygen by the vegetables. Since there is no simple method whereby a uniform atmospheric pressure can be maintained, correc-

tions had to be applied. This was done by setting up a second chamber of the same size and thickness of glass as the chamber (E). Pressure changes occurring during each run were recorded on the gauge of this control chamber; thus it was possible to calculate accurately necessary corrections for the volume of gases occupying the respiration chamber and oxygen cylinder. The volume of oxygen consumed was calculated to standard conditions on the basis of the atmospheric pressure and temperature prevailing at the beginning of each run.

Another source of error was eliminated by allowing equilibrium to establish itself between the carbon dioxide in the chamber and the absorbing alkali before the initial oxygen reading was taken. Actually, a true equilibrium is never reached because the absorbing power of the hydroxide diminishes as its concentration decreases. Consequently, the partial pressure of carbon dioxide in the chamber increases throughout the run. Preliminary experiments showed, however, that during the first four hours the concentration rose to one per cent. or less, depending on the actual rate of respiration. Thereafter, the rate of increase in the partial pressure of carbon dioxide became so small that it could be neglected. In the course of actual experimentation, the funnel (F) was drained four hours after the apparatus was set up and fresh sodium hydroxide was added after which the initial reading was taken.

The corrected value for the volume of oxygen consumed in respiration was calculated according to the formula:

$$V_o = V_1 + KV_1 + \frac{P}{P_1} \times V_c \times \frac{P_1 - PH_2O}{760} \times \frac{273}{T}$$

where V_o = corrected volume of oxygen reduced to standard conditions.

V_1 = volume of oxygen displaced by water.

V_c = free volume of the system at the end of the experiment.

K = constant to correct for differences in the solubility of oxygen and nitrogen in water when in equilibrium with air and pure oxygen at the temperature T.

P = pressure change as measured in the check chamber.

P_1 = initial barometric pressure.

PH_2O = vapor pressure of water at the temperature T.

T = temperature in degrees of absolute temperature.

Respiration studies were carried out in three rooms in which temperatures of 0.5, 10.0, and 24.0° C. were maintained. In order to keep temperature fluctuations within 1° C., it was found necessary to enclose the apparatus in a large box well insulated with fiber board. Light was excluded from the vegetables except for brief periods when the apparatus was assembled or when readings were taken.

Immediately after harvesting the vegetables were cleaned, weighed, and aliquot lots distributed in the three rooms. Usually the first determinations of the respiration rate were made 6 hours after harvest. There were two

exceptions, however. For greenhouse cucumbers, which were obtained from a grower in Indiana, the first determination was delayed three days. Potatoes used in these experiments had been harvested three weeks earlier and in the meantime they had been held at an approximate average temperature of 13° C.

Depending on the kind of vegetable involved and the temperature of the storage room, each respiration run lasted from five hours to three days. During this period, the vegetables were necessarily exposed to an atmosphere saturated with water vapor. Between experiments, they were kept in the same room and at the same temperature, but at a relative humidity considerably below that of the respiration chambers. In some vegetables, this resulted in severe wilting, a fact which must be taken into account when interpreting the results of these respiration studies. Depending on the expected storage life at each of the three temperatures, determinations of the respiration rate were repeated at intervals varying from one day to one month until the samples showed signs of internal breakdown or infection with disease organisms.

All respiration data were expressed on the basis of the original fresh weight. It was feared that calculations on the basis of fresh weight at successive periods would yield misleading results, since changes in the fresh weight are caused primarily by the loss of water in transpiration, whereas the actual dry weight of the samples decreases but little.

The kinds of vegetables and the particular variety used in these respiration studies were as follows:

Asparagus (*Asparagus officinalis*); var. Mary Washington.
Peas (*Pisum sativum*); var. Laxton Progress.
Snap beans (*Phaseolus vulgaris*); var. Tendergreen.
Spinach (*Spinacia oleracea*); var. Long Standing Bloomsdale.
Lettuce (*Lactuca sativa*); var. New York (Imperial 44).
Carrots (*Daucus carota*); var. Red Core Chantenay.
Peppers (*Capsicum frutescens*); var. Windsor A.
Tomatoes (*Lycopersicum esculentum*); var. Marglobe.
Cucumbers (*Cucumis sativus*); var. Davis Perfect.
Potatoes (*Solanum tuberosum*); var. Rural.

It will be noticed that this list includes vegetables representing different plant organs such as shoots, roots, tubers, fruits, and leaves. Also, these vegetables have a wide range of respiratory activity, some having a respiration rate more than 50 times as high as others.

Results and discussion

Factors affecting the respiration rate

Following the conventional method of expressing the degree of respiratory activity, the results of these experiments are reported in terms of car-

bon dioxide production. Calculations based on oxygen consumption would have led to the same general conclusions with respect to the relative respiration rates of the different vegetables. Considering first the rates at 24° C., shown in figures 2 and 3, it will be noticed that in general the rates declined rapidly during the first few days of storage. Thereafter, the trend became irregular, some vegetables showing a further decrease, others an upward trend in respiratory activity. Striking differences are apparent in the relative rates of the ten vegetables studied. To mention two extremes, the initial rate of asparagus was found to be 59 times as high as that of potatoes. The trends in respiratory activity at 10° C. are shown in figures 4 and 5 and those at 0.5° C. in figures 6 and 7. While the decline in respiration rates followed the same pattern as it did at 24° C., the general level of activity became decidedly lower as the storage temperature decreased.

Unquestionably, the actual respiration rate observed in each instance is the integrated result of several factors, but an explanation of the behavior of any one vegetable must rest on pure speculation. Nothing more is possible than to point out some of the factors which appear to play a prominent rôle in the respiration process.

While most of the available evidence supports the theory that, of the different forms of sugar found in plant material, only glucose serves as the ultimate substrate in respiration, data have been presented by BARKER (**2**) which suggest strongly that, in potatoes at least, the gamma-fructose part of the sucrose molecule is oxidized before glucose enters the respiration process. Regardless of the types of sugar which may serve as substrates, the observed differences in the initial respiration rate of different vegetables cannot be explained on the basis of the law of mass action. Examination of table I furnishes convincing proof that no correlation exists between respiratory activity of different vegetables and their content of either glucose or total sugars. This lack of correlation is by no means to be taken as evidence that the law of mass action plays no rôle in determining respiration rates; its effect may merely be masked by the influence of other factors of greater importance. In considering the respiration curves of individual vegetables, many of the internal factors remain nearly constant in their effect on respiration and it becomes then possible to explain the gradual decline in respiration rates by means of the law of mass action. Still, the view may be taken that this decline in rate is the effect of gradual aging and slow disintegration of the cells.

Little is known about the kinds and quantities of enzymes taking part in the respiration process directly or indirectly. It seems likely that this factor is the most important one of all. In fact, differences in the respiratory activity of the various plant organs may in the last analysis be attributed to deviations in enzyme activity.

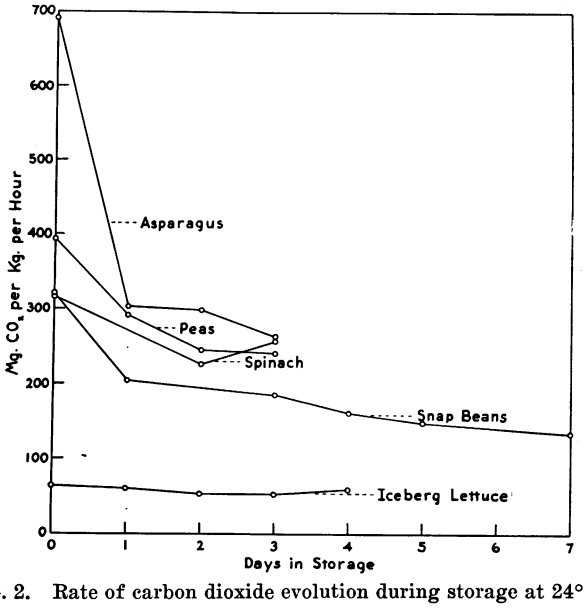

FIG. 2. Rate of carbon dioxide evolution during storage at 24° C.

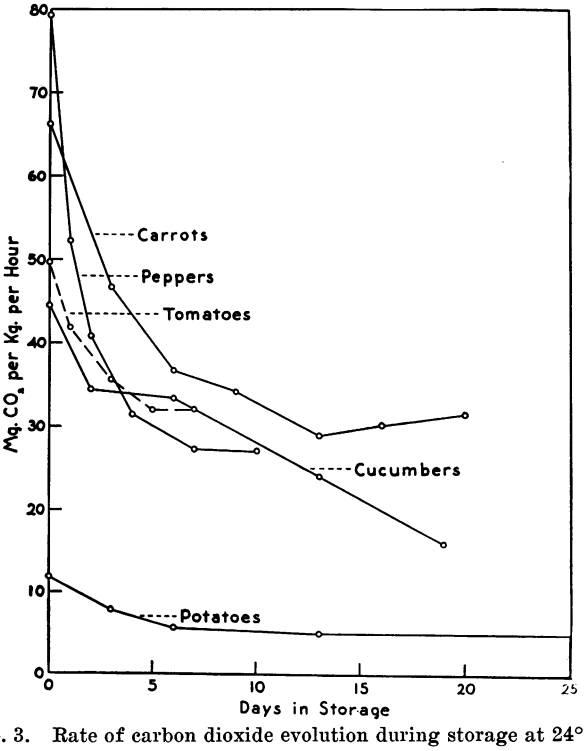

FIG. 3. Rate of carbon dioxide evolution during storage at 24° C.

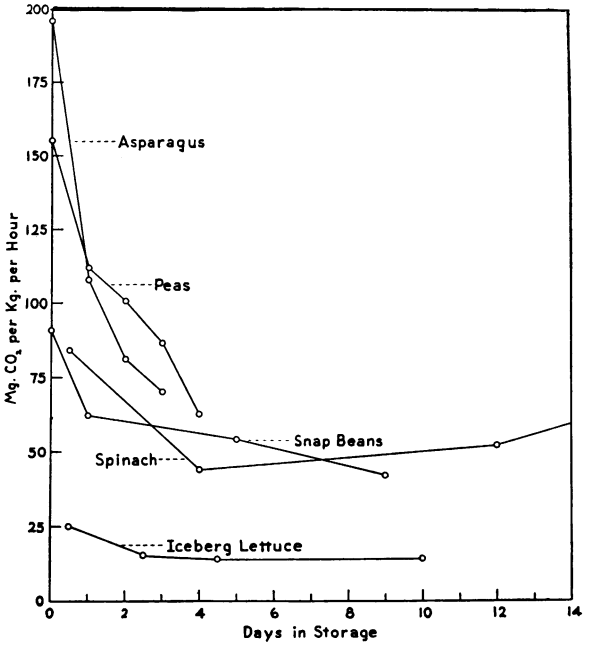

FIG. 4. Rate of carbon dioxide evolution during storage at 10° C.

A factor of minor importance is the permeability of the epidermis to carbon dioxide and oxygen. Because of the dissimilarity in the epidermal

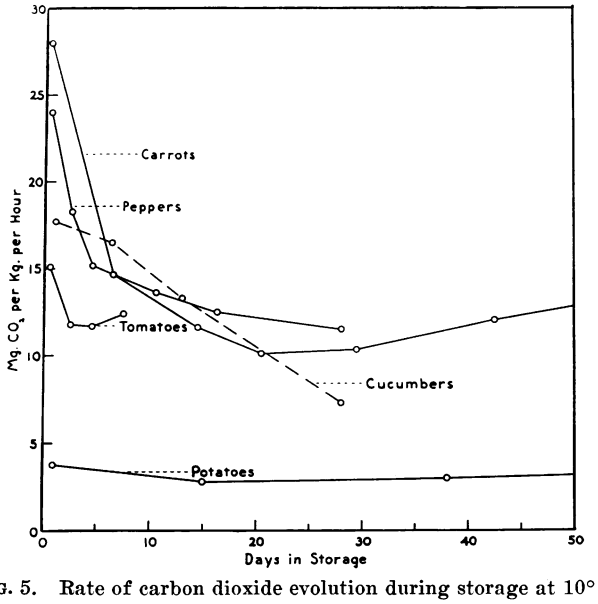

FIG. 5. Rate of carbon dioxide evolution during storage at 10° C.

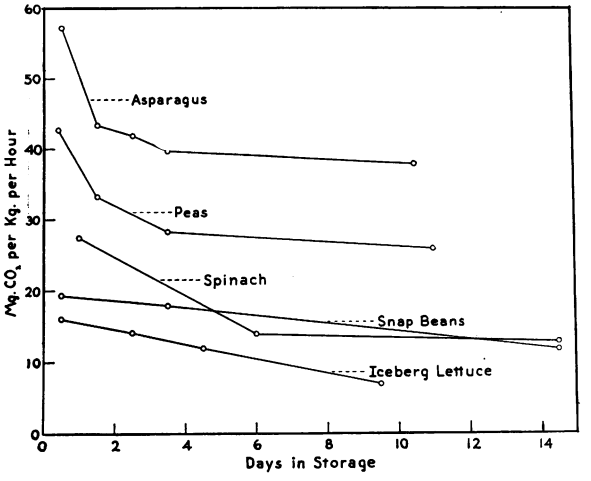

FIG. 6. Rate of carbon dioxide evolution during storage at 0.5° C.

structure of vegetables the rate at which gaseous exchange can take place should vary correspondingly.

It must be admitted that little is to be gained by merely enumerating the various factors which may influence the respiration rate of plant material. Not until many additional data become available to show quantitatively the relationship between each one of these factors and respiration rate will it be

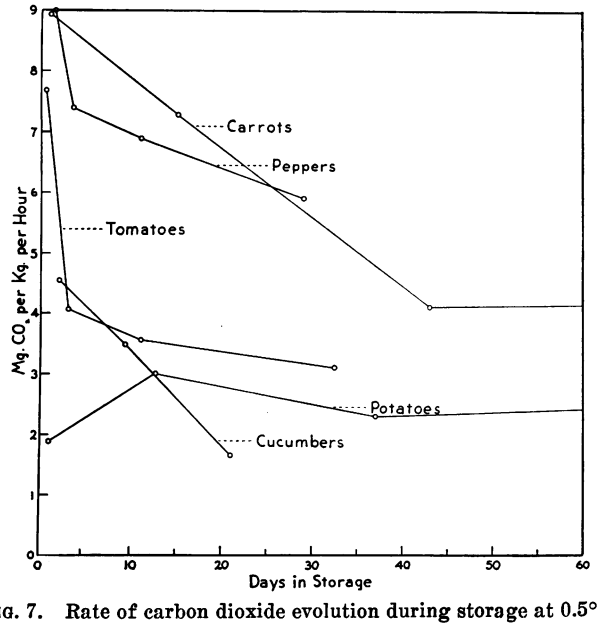

FIG. 7. Rate of carbon dioxide evolution during storage at 0.5° C.

possible to state with any degree of assurance why the wide variability in respiratory activity exists.

As stated before, the respiration rate falls off as the storage period progresses. This decline is most rapid during the first few days and usually diminishes as time goes on; also, the decrease in respiratory activity is more rapid at the higher than at the lower temperatures. Regardless of whether this decline is attributed to mass action or to other physiological processes associated with the aging of the tissue, it is interesting to find that the general trend of the respiration curves can easily be upset when a new factor becomes operative. Instances of this type occurred during the storage of lettuce, spinach, carrots, and potatoes at 24° C. and to some extent at 10° C. While the respiration rate of these vegetables declined during the first few days a subsequent rise in the rate became apparent toward the latter part of the storage period. At first it was believed that this secondary rise in spinach and lettuce might be attributable to the growth of microorganisms. Close examination, however, showed them to be free of decay spots. Instead it was found that the increase in respiration activity was associated with new growth. Both lettuce and spinach had begun to develop new growing points which probably would have developed into seedstalks had it been possible to prevent ultimate breakdown from other causes. Similarly, carrots and potatoes had begun to produce sprouts at the time the decline in respiration rate had ceased. It was also noticed that changes in the trend of respiratory activity did not occur until the sprouts had reached a length of two centimeters or more. These observations make it evident that the secondary rise in respiration rate is the result of the high rate of metabolic activity of the newly developed tissue itself and not the effect of the mere initiation of new growth.

Substrate used in respiration

Although no attempt was made to trace metabolic changes associated with respiration in these experiments, it is possible to make certain deductions from the available data. The respiration experiments of Asparagus were accompanied by chemical analyses of comparable samples taken at harvest time and again after three days of storage at 24° C. The following table shows the results of the analyses for total sugar content:

	Grams total sugar per 100 grams original fresh weight
At the beginning of the experiment	1.87
After three days of storage at 24° C.	1.06
Loss in total sugars	0.81

Sugar losses were compared with the amount of glucose corresponding to the carbon dioxide produced in Asparagus held under identical conditions for the same interval. From the data given in figure 2, it was calcu-

lated that during this period 2.57 gm. of carbon dioxide were produced per 100 gm. of fresh material and this quantity is equivalent to 1.75 gm. of glucose. Obviously, the quantity of total sugars lost can account for only one-half of the carbon dioxide given off. The conclusion seems inevitable that a large share of this substrate was furnished by substances other than sugars. The discrepancy between sugar losses and carbon dioxide evolution is further aggravated by the fact that, according to BISSON and JONES (**5**), there is a substantial gain of crude fibre in storage and this gain must be ascribed to a polymerization of sugars, a factor which tends to increase still further the quantity of the sugar equivalent of carbon dioxide unaccounted for. Starch being absent in Asparagus and fats being available in minute quantities only, one must conclude that protein was utilized in respiration to a considerable extent.

Many textbooks on plant physiology contain statements to the effect that proteins may undergo decomposition and become available for respiration, but it is generally assumed that this process occurs only if plants are in a starved condition; that is, when all or most of the available carbohydrate reserve has been consumed. The present data suggest that one-half of the substrate was furnished by the hydrolysis of proteins and deaminization of amino-acids at a time when more than one-half of the original sugar content was still present. Further evidence in support of the theory of protein utilization is given by the low values for the respiratory quotient, shown in table III, which at 24° C. dropped to less than 0.9 after the first day and rose again to 0.95 on the last day of storage. Depending on their particular composition, proteins give a respiratory quotient of 0.80 to 0.82. Proteins and sugars being utilized in respiration at equal rates would give a quotient of 0.9 or slightly higher, a value which agrees reasonably well with the quotient actually observed.

The metabolism of Asparagus in storage is not a unique case, however. On the basis of detailed chemical analysis, YEMM (**17**) proved conclusively that some of the protein in detached barley leaves held in the dark was decomposed and utilized in the respiration process during the first 12 hours of storage, long before the available carbohydrate reserve was depleted. VICKERY, PUCHER, WAKEMAN, and LEAVENWORTH (**16**) obtained indirect evidence of the utilization of leaf proteins of rhubarb during respiration, and CHIBNALL (**6**), discussing protein metabolism in connection with respiration, comes to the conclusion that protein destruction and the utilization of the products of hydrolysis in respiration occurs more frequently and at an earlier stage than had been heretofore supposed.

As illustrated in table I, neither the concentration of sugars nor that of total carbohydrates in the various vegetables is related to their initial respiration rates. A comparison of the respiration curves for peas and snap beans further shows that sugar concentration alone does not materially alter

TABLE I

GLUCOSE, TOTAL SUGARS, AND TOTAL CARBOHYDRATE CONTENT OF TEN VEGETABLES ON A FRESH WEIGHT BASIS AND THEIR INITIAL RESPIRATION RATE AT 24° C.*

VEGETABLE	GLUCOSE	TOTAL SUGARS	TOTAL CARBOHYDRATES	RESPIRATION RATE PER HOUR PER KG.
	%	%	%	*mg. CO_2*
Asparagus	1.80	1.9	1.9	692.0
Peas	0.90	6.3	8.3	394.0
Snap beans	2.50	2.7	3.8	321.0
Spinach	1.20	3.0	4.1	318.0
Peppers	?	2.1	6.3	78.8
Carrots	3.02	6.8	6.8	66.2
Iceberg lettuce	?	2.2	2.2	64.2
Tomatoes	3.60	3.6	3.7	49.6
Cucumbers	1.90	2.6	2.6	44.5
Potatoes	0.30	0.9	15.6	11.8

* Data compiled from various sources in the literature and from unpublished analyses obtained by the writer.

the rate at which the respiratory activity decreases in any one vegetable (fig. 2). As is generally known, the sugar content of peas at 24° C. is rapidly depleted, whereas PARKER and STUART (**14**) demonstrated that the percentage of sugars in snap beans remains nearly constant. In spite of the wide differences in the sugar concentration of these two vegetables after several days of storage, the rate at which the respiration rate of each diminished was nearly the same. Potatoes shifted from a temperature of 12° C. to 0.5° (fig. 7) behaved differently; at first the respiration rate increased, then dropped again and assumed a nearly constant level after 37 days. Based on the results of HOPKINS (**10**), one could attribute the initial rise in respiration rate to the shift of starch to sugar which takes place at that temperature. APPLEMAN and SMITH (**1**), however, found that potato tubers shifted from a low temperature to 30° C. had a high initial respiration rate which declined rapidly in spite of the fact that at this temperature the concentration of total sugars actually increased for 10 days. All available evidence makes it extremely doubtful, therefore, that a shift in the sugar-starch equilibrium of plant material has a direct effect on the respiration rate.

TEMPERATURE COEFFICIENTS

The relationship between temperature and respiration rate is usually expressed in terms of Q_{10} values which indicate the ratio between reaction rates at intervals of 10° C. Since in these experiments, temperature intervals were 9.5° and 14.0° C., respectively, it became necessary to recalculate the data on the basis of a 10° temperature range. This was done by applying the formula

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}}$$

where T_1 and T_2 are the lower and upper temperature levels and R_1 and R_2 the corresponding respiration rates based on carbon dioxide production. Using this method, it was possible to compare the acceleration of the respiration rate with temperature for different temperature ranges.

There are certain limitations in the use of Q_{10} values for respiration rates. First of all, such values, in order to have any meaning, can be applied to the initial rates only, since in comparisons at any later stage one would be dealing with vegetables of different physiological age and different chemical composition. Furthermore, one must remember that temperature coefficients expressed as Q_{10} values represent averages only and there is good reason to believe that within the observed range the rate of acceleration is by no means uniform.

In table II, the Q_{10} values for two temperature ranges are arranged in descending order of respiratory activity of the vegetables as determined for the initial rate at 24° C. It is obvious that there is a complete lack of correlation between the initial respiration rate at a given temperature and the effect that a change in temperature produces on respiratory activity. The

TABLE II

Q_{10} VALUES FOR RESPIRATION OF TEN VEGETABLES

Vegetable	Temperature range	
	0.5°–10.0° C.	10.0°–24.0° C.
Asparagus	3.7	2.5
Peas	3.9	2.0
Snap beans	5.1	2.5
Spinach	3.2	2.6
Peppers	2.8	2.3
Carrots	3.3	1.9
Iceberg lettuce	1.6	2.0
Tomatoes	2.0	2.3
Cucumbers	4.2	1.9
Potatoes	2.1	2.2

magnitude of the Q_{10} values within the range of 0.5° to 24° C. varies from 1.6 to 5.1, indicating that VAN'T HOFF'S rule applies to respiration rates only very roughly. Still, this range of Q_{10} values is much narrower than that found for chemical reactions involving carbohydrate metabolism in vegetables where the writer found values as high as 27.5 (**15**).

The calculated Q_{10} values vary not only with different vegetables, but also with the temperature range at which they were determined. In seven out of ten vegetables, the values were lower at the upper temperature range. This relationship is in accord with the general observation that the rate of acceleration of biological reactions diminishes as higher temperatures are approached. On the other hand, the findings stand in contrast to the results

of GERHART (7) and GORE (8) who, working with various fruits, failed to notice any decided falling off in the acceleration of respiration until a temperature of 32° C. was attained.

In interpreting the calculated Q_{10} values, it is well to distinguish between the direct and indirect temperature effects. The rate of increase in respiration with rising temperature would probably follow a comparatively smooth curve were it not for the fact that any shift from one temperature to another involves pronounced changes in plant metabolism. Such changes do not necessarily follow VAN'T HOFF'S rule; in fact, a complete reversal in the reaction equilibrium may take place as is illustrated by the sugar-starch equilibrium of potato tubers at different temperatures. Little is known of the extent to which shifts in the metabolic course with changing temperature influence the respiration rate. One may reasonably assume, however, that the existing variations in the Q_{10} values found are in part caused indirectly by the effect that temperature changes have on plant metabolism.

RESPIRATORY QUOTIENT AND SUBSTRATES USED IN RESPIRATION

Certain deductions concerning the course of respiration can be made if the available data show not only the rate of carbon dioxide production, but also the quantity of oxygen consumed. In fact, much valuable information about the mechanism of plant respiration has been obtained from experiments in which the respiratory quotient was the principal criterion of the effect that certain factors, such as anesthetics, had on the respiratory quotient under controlled conditions.

In the present study, calculations of the respiratory quotient were included primarily for the purpose of ascertaining to what extent substrates, other than carbohydrates, were involved in the respiration process. It must be admitted, however, that the respiratory quotient alone cannot give any definite information concerning either the course of respiration or the substrate utilized. In no way can the magnitude of the respiratory quotient be considered an expression of the degree to which the oxidation process has been completed. Depending on whether organic acids or fats and proteins serve as substrates, a quotient above or below one may be obtained by complete oxidation to carbon dioxide and water. Likewise, under partial anaerobic conditions some of the sugar may be converted to alcohol and carbon dioxide or it may be oxidized to organic acids; the corresponding respiratory quotients would be above one in the former, and below one in the latter case. The interpretation of the respiratory quotient is further complicated by the fact that several substances may be involved in the respiration process simultaneously. If, for instance, proteins, sugars and organic acids serve in equal molar proportions as substrates for the complete oxidation to carbon dioxide and water, the observed quotient would be close to

unity, a value similar to that which would be obtained if only sugars were involved in the respiration process. Consequently, it is possible to draw definite conclusions from the observed respiratory quotients only if the studies are supplemented by detailed chemical analyses serving as a balance sheet to show exactly the net loss or gain in the substrates and end-products of respiration.

The data in tables III, IV, and V are presented, therefore, only for the purpose of suggesting instances where an unusual behavior in the respiration process is indicated. Subject to a few exceptions, certain trends are apparent. For most vegetables, a quotient fairly close to unity was observed. In general, the respiratory quotient was highest immediately after harvest. As the storage period progressed, the quotient drifted to slightly lower levels. A definite relationship between the storage temperature and the respiratory quotient was also indicated; higher values were usually obtained in the upper temperature range.

Considering the behavior of each vegetable separately, the possibility suggests itself that the respiratory quotient in some way is connected with the intensity of respiration. It is not unlikely that rapid utilization of organic acids occurs whenever the rate of respiration is high, which would result in a quotient above unity. It may also be that protein decomposition plays an increasingly greater rôle toward the end of the storage period, tending to depress the quotient obtained. Detailed chemical analyses of plant tissue in storage are required before any such causal relationship can be established as fact.

Some speculation may be permitted to explain the behavior of those few crops that show marked deviations in their respiratory quotients from unity. The behavior of Asparagus has been discussed earlier. Two other vegetables showing even more pronounced abnormalities are spinach and potatoes, both having unusually low quotients, especially at 0.5° C. The unusual behavior of spinach may be explained by assuming that leaf protein was decomposed and utilized in respiration to a large extent. There is also a remote possibility that during storage, part of the oxygen was used in the formation of organic acids. According to compilations by KOHMAN (**11**) the oxalic acid content of fresh spinach may vary from 0.29 to 0.69 per cent. It was calculated that the excess quantity of oxygen consumed during a 10-day storage period at 0.5° C. would yield only 0.1 gm. of additional oxalic acid for each 100 gm. of fresh weight.

No definite explanation can be offered for the unusually low quotients exhibited by potatoes in storage. The values obtained agree closely with those of BENNETT and BARTHOLOMEW (**3**) who calculated quotients as low as 0.49 for tubers stored at 7.5° C. In both sets of data, the lowest values were found at the beginning of the storage period; later, a gradual increase

TABLE III

RESPIRATORY QUOTIENT OF TEN VEGETABLES IN STORAGE AT 24° C.

VEGETABLE	DAYS IN STORAGE												
	0	1	2	3	4	5	6	7	8	10	12	19	30
Asparagus	1.04	0.89	0.88	0.95	.....	.....	.....	.....	.....	.....	.....	.....	.....
Peas	1.32	1.05	1.05	1.06	.....	.....	.....	.....	.....	.....	.....	.....	.....
Snap beans	1.14	1.01	.....	1.00	0.99	1.01	.....	1.01	.....	.....	.....	.....	.....
Spinach	0.94	.....	0.85	0.83	.....	.....	.....	.....	.....	.....	.....	.....	.....
Peppers	1.12	1.02	0.97	.....	0.90	.....	.....	0.83	.....	0.88	.....	.....	.....
Carrots	1.10	.....	.....	1.05	.....	.....	1.07	.....	1.07	.....	1.10	1.18	.....
Iceberg lettuce	1.12	1.05	1.07	0.99	1.02	.....	.....	.....	.....	.....	.....	.....	.....
Tomatoes	1.11	1.13	1.11	1.09	.....	1.12	.....	1.13	.....	.....	.....	.....	.....
Cucumbers	1.01	.....	1.07	.....	.....	.....	1.15	.....	.....	.....	1.08	0.91	.....
Potatoes	1.02	.....	.....	0.83	.....	.....	0.79	.....	.....	.....	0.75	.....	0.91

TABLE IV

RESPIRATORY QUOTIENT OF TEN VEGETABLES IN STORAGE AT 10° C.

VEGETABLE	DAYS IN STORAGE										
	0	1	2	3	4	5–7	10–12	13–18	30–40	41–60	61–80
Asparagus	1.03	0.93	0.83	0.86	.....	.....	.....	.....	.....	.....	.....
Peas	1.13	1.11	1.07	1.05	1.00	.....	.....	.....	.....	.....	.....
Snap beans	1.08	0.98	.....	.....	.....	1.01	1.00	.....	.....	.....	.....
Spinach	0.90	.....	.....	.....	0.87	.....	0.84	0.86	.....	.....	.....
Peppers	1.27	.....	1.01	.....	1.02	.....	1.01	0.91	0.88	.....	.....
Carrots	1.08	.....	.....	.....	.....	0.89	.....	0.99	0.94	1.01	1.01
Iceberg lettuce	1.09	.....	0.93	.....	0.94	.....	1.00	.....	.....	.....	.....
Tomatoes	1.39	.....	1.08	.....	1.04	1.06	.....	.....	.....	.....	.....
Cucumbers	1.01	.....	.....	.....	.....	1.03	.....	1.06	1.10	.....	.....
Potatoes	.....	0.86	.....	.....	.....	.....	.....	0.83	0.86	.....	0.99

TABLE V

RESPIRATORY QUOTIENT OF TEN VEGETABLES IN STORAGE AT 0.5° C.

VEGETABLE	DAYS IN STORAGE											
	1	2	3	4–6	6–8	8–10	11–15	16–20	21–30	31–40	41–60	61–100
Asparagus	0.98	0.96	1.00	0.99	.....	0.95	.....	.....	.....	.....	.....	.....
Peas	1.00	.....	1.07	0.98	.....	.....	0.96	.....	.....	.....	.....	.....
Snap beans	0.94	.....	0.90	.....	.....	.....	0.96	.....	.....	.....	.....	.....
Spinach	0.85	.....	.....	.....	0.79	.....	0.73	.....	.....	0.80	.....	.....
Peppers	0.96	.....	0.96	.....	.....	.....	0.95	0.95	0.97	0.96	.....	.....
Carrots	0.92	.....	.....	.....	.....	.....	0.92	.....	.....	.....	1.07	1.16
Iceberg lettuce	0.88	.....	0.84	0.97	.....	0.98	.....	.....	.....	.....	.....	.....
Tomatoes	1.11	.....	0.91	.....	0.92	.....	0.97	.....	.....	1.02	.....	.....
Cucumbers	.....	0.97	.....	.....	.....	0.98	.....	.....	0.88	.....	.....	.....
Potatoes	0.45	.....	.....	.....	.....	.....	0.58	.....	.....	.....	0.56	0.66

was noticed, but even after 123 days of storage at 0.5° C. the writer found a respiratory quotient of only 0.78. Most surprising is the fact that such a wide ratio between oxygen consumption and carbon dioxide evolution can be maintained for a period of several months. Surely the excessively low quotients cannot be explained on the basis of differential permeability of the epidermis to carbon dioxide and oxygen. If such a difference did exist, its effect would soon be overcome by an increase in the partial pressure of carbon dioxide within the tissue. Equally unlikely is the assumption that the utilization of fats and proteins caused the abnormally low quotients. If these substances had been used one should expect a quotient of 0.7 to 0.8, values much higher than those actually found. Perhaps the most plausible explanation can be based on the theory that throughout the storage period part of the carbohydrates are oxidized incompletely to organic acids. The actual quantity of acids accumulated would not be unreasonably large. Assuming an average respiration rate of 2.5 milligrams of carbon dioxide per kilogram per hour and an average quotient of 0.6, the total quantity of oxygen consumed in excess of the corresponding amount of carbon dioxide evolved would be only 0.288 gm. per 100 gm. fresh weight in a period of 100 days. This quantity would be sufficient to form 1.2 gm. of malic acid by oxidation of sugar. The accumulation of that quantity of organic acid is not unlikely. At any rate, of all the possibilities examined, this theory appears to offer the most probable explanation. The only conclusion that can be drawn from the available data is that the respiration of potatoes at low temperatures involves not only the simple oxidation of sugars to carbon dioxide and water, but also metabolic processes of greater complexity.

Low temperature injury and respiration

Low temperature injury or surface pitting is a physiological disorder which occurs in many fruits and vegetables after exposure to temperatures slightly above the freezing point for a period of one week or longer. Since the first investigation of this type of injury by Nelson (**13**), it has been suggested that surface pitting is associated with an abnormal course of respiration. Nelson demonstrated that the same kind of injury can be produced in some vegetables at room temperature by reducing the oxygen supply of the surrounding air. From the results of his experiments he concluded that the ultimate cause of pitting is the inability of the tissue to obtain or utilize sufficient oxygen for normal respiration when held at low temperatures. If this theory is correct, one should expect marked deviations in the respiratory quotient at 0.5° C. in those products which ordinarily exhibit this type of physiological disorder. Of the vegetables included in these experiments, cucumbers, peppers, and snap beans developed typical symptoms of pitting at 0.5° C. after periods varying from 10 to 20 days. Still, the data in table V suggest no unusual behavior during respiration at that

temperature. The calculated quotient always remains below unity, showing that actually more oxygen is consumed than would be required for the normal oxidation of sugars to carbon dioxide and water. Comparisons of the respiratory quotients with those observed at higher temperatures or with the quotients of other vegetables showing no injury at 0.5° C., fail to show any relationship which would suggest an abnormal course of respiration. While it must be admitted that these data do not furnish conclusive evidence to disprove the theory of NELSON, they render it extremely doubtful that suboxidation is the direct cause of low temperature injury.

Summary

Wide variations were found in the respiration rate of 10 different vegetables. For example, at 24° C. the initial respiration rate of Asparagus was found to be 59 times as high as that of potatoes.

No correlation could be found between respiration rates of different vegetables and their glucose content or carbohydrate reserve. The type of tissue, whether actively growing at time of harvest, or whether representing a storage organ, appeared to play a dominant rôle in determining the respiration rate of vegetables held under identical conditions.

In general, the respiration rate declined gradually with time at all temperatures. This decline may be attributed to the effect of the law of mass action or to a general aging effect.

Carbon dioxide production of Asparagus at 24° C. exceeded corresponding sugar losses as determined by chemical analysis of comparable samples. The results suggest that protein is decomposed and utilized in respiration to a considerable extent.

Temperature coefficients were calculated for two temperature ranges, 0.5° to 10°, and 10° to 24° C. The corresponding Q_{10} values varied from 1.6 to 5.1, usually being lower in the upper temperature range.

Respiratory quotients in general were highest soon after harvest, and with few exceptions smaller values were found at the lower temperature levels.

Spinach and potatoes gave unusually low respiratory quotients, especially at 0.5° C. As a possible explanation, it is suggested that in these vegetables, carbohydrates are converted to organic acids.

Vegetables which developed low temperature injury at 0.5° C. failed to show any unusual respiratory quotients. Based on these data, it appears unlikely that low temperature injury is the result of suboxidation.

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